## NEW TAXA FROM BRAZIL AND GUYANA IN THE GENUS HYMENAEA (LEGUMINOSAE, CAESALPINIOIDEAE)

YIN-TSE LEE AND JEAN H. LANGENHEIM

The Genus Hymenaea (Leguminosae, Caesalpinioideae, Detarieae \*) is presently considered to have 16 species distributed from central Mexico, throughout Central America, the West Indies and all of the South American countries except Uruguay and Chile (Langenheim, Lee, & Martin, 1970, 1971; Langenheim, 1972). The Amazon Basin appears to be its center of distribution and its closest relative is the east African genus Trachylobium (Langenheim, 1972; Langenheim, Martin, & Lee, 1972).

The four taxa presented here occur in evergreen rainforest habitats in Brazil and Guyana (Figure 1). A previously undescribed species of Hymenaea and a new variety of H. oblongifolia Huber occur in the Atlantic coastal forests. Both of these taxa occur in southern Bahia, with the new variety having been collected also in more northerly sites in Pernambuco. Hymenaea oblongifolia previously has been known only from the heavy rainfall areas (over 2000 mm. annually) in the eastern and western portions of the Amazon Basin.

The other taxa to be discussed are *H. palustris* Ducke and *H. davisii* Sandwith, which are to be reduced to varieties of *H. oblongifolia*. Hymenaea palustris has a distribution very similar to that of *H. oblongifolia* in the Amazon Basin, but is locally isolated from it by a habitat difference. Hymenaea oblongifolia occurs primarily in the várzea (periodically inundated area), whereas *H. palustris* occurs principally in the continually wet igapó (swamp forest). Hymenaea davisii occurs along streams in the Wallaba (Eperua) forest in Guyana.

The relationship of the flora of the Amazonian rainforest ("hylaea") and the Brazilian Atlantic coastal rainforests, occurring from Pernambuco to the region around Rio de Janeiro, has aroused considerable interest for some time (Ducke, 1959; Andrade-Lima, 1953; Rizzini, 1963, 1967). Rizzini (1967) indicated that 277 genera occur both in the Amazonian and Atlantic rainforests. Usually a genus which is represented by one or a few species in the Atlantic forest is found to have several or many species in the Amazonian hylaea. The "Hylaea Bahiana," a region of forest occupying Tertiary plateaus in the south of Bahia and north of Espirito Santo, was once thought to be composed almost entirely of Amazonian species (Rizzini, 1963). More recent studies, however,

<sup>\*</sup> In previous work (Langenheim, 1972), we have used the tribal designation of Cynometreae Bentham (1840) emend. Léonard (1957). Recently Heywood (1971) has presented de Candolle's (1825) name Detarieae which has priority over Bentham's name Cynometreae.

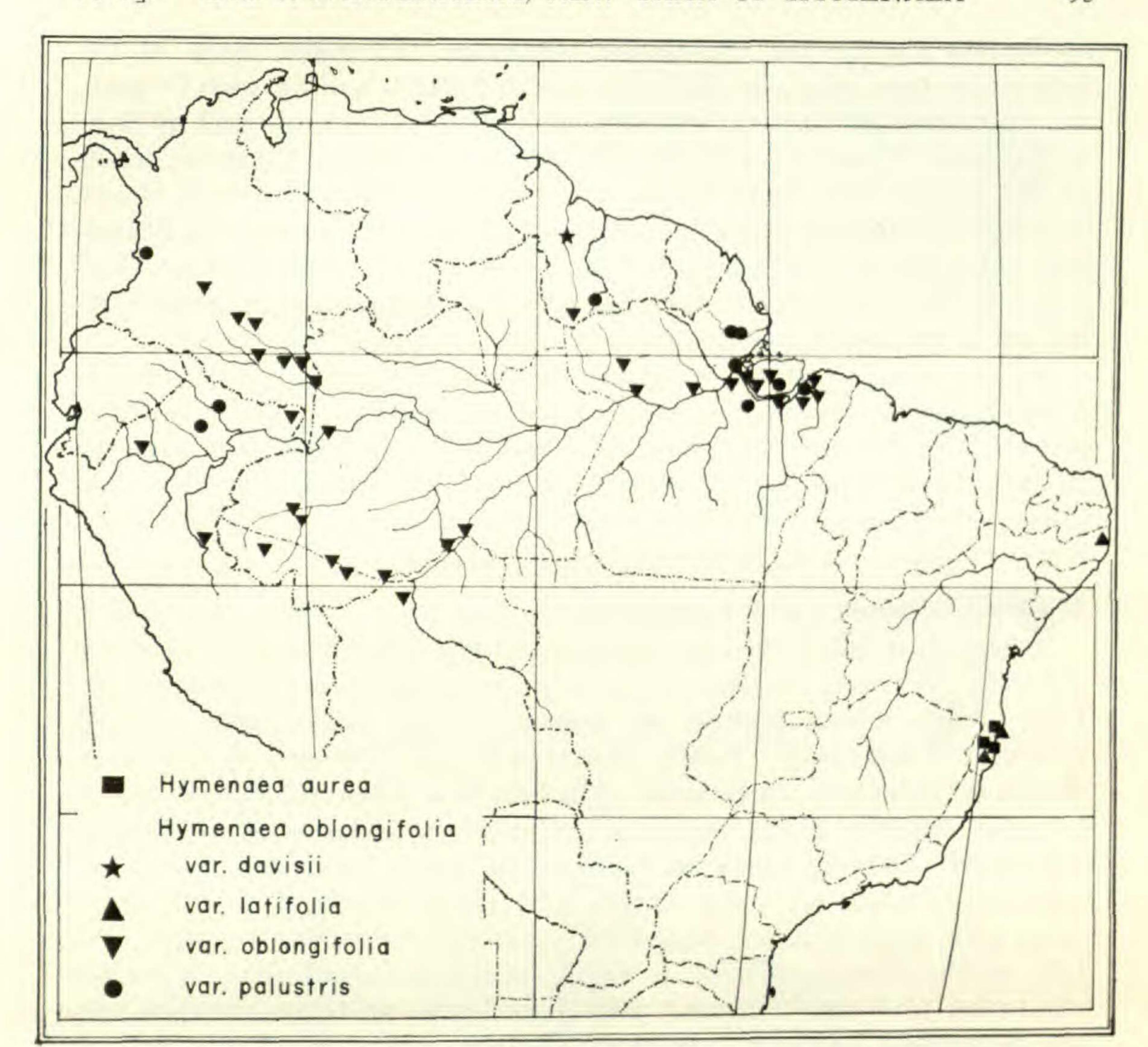


FIGURE 1. Map showing distribution of Hymenaea aurea, H. oblongifolia and its varieties.

have shown this area to have Amazonian, Atlantic, and endemic elements (Rizzini, 1967). Andrade-Lima (1953) also noted the high degree of similarity of this Bahian hylaea to that of the Amazonian terra firma and pointed to the role of high, annually well-distributed rainfall (2,000 mm. or more) in maintaining the two vegetation types. Vanzolini and Williams (1970) also have recorded the disjunct distribution in the Atlantic forest of "deep forest animals" from the Amazonian hylaea. The occurrence of Amazonian elements in these Atlantic forests, as well as in the central Brazilian cerrados and cerradãos and the northwestern caatinga, is a present-day indication of the previously more extensively distributed moist tropical vegetation and associated faunas that occurred as far south as central Patagonia in early Tertiary time (Menéndez, 1969; Simpson, 1969). During the Eocene epoch tropical rainforest vegetation probably reached its maximum development, extending to at least 50° north and attained almost double its present distribution (Wolfe, 1971, pers. comm., 1972). Progressive drying trends from Miocene to the present, with some

oscillations during the Pleistocene, restricted the major body of the Amazonian-type hylaea to the basins of the Amazon and the high Orinoco, the watersheds of Guyana, Surinam, and French Guiana as well as those of the lower Tocantins and Rio Pindaré in Maranhão. However, relicts of this hylaea flora occur locally throughout central and coastal Brazil. Marine transgressions along coastal Brazil during the Pliocene and Pleistocene (Harrington, 1962) probably further altered the coastal hylaea. Elements of the older tropical flora, particularly, appear to have found a refugium in the southern Bahia-northern Espirito Santo "tabuleiro."

Rizzini (1967) lists H. courbaril, the most widespread species of Hymenaea, as occurring in these Atlantic forests. We have found it in Bahia in both the evergreen rainforest and semideciduous forest. Its presence in both forest types is not unexpected since this species occupies evergreen, semideciduous, and deciduous forests, savannah, and thorn scrub

essentially throughout the distribution of the genus.

Hymenaea aurea Lee & Langenheim, sp. nov. FIGURES 1 and 2. Arbor usque ad 28 m. alta, diametro 90 cm. Rami juniores, alabastra, petioli ac folia tomento denso aureo-luteo, in senectute aureo-brunneo, obtecti. Rami vetusti brunnei fel argenteo-cinerei excorticantes. Petioli breves, 3-7 mm. longi. Foliola obovato-oblonga (5-9 cm. × 2-4 cm.), obtusa vel apiculata, supra nitida, pilis brevibus, subtus pilis densis aureobrunneis obtecta. Costa superficiei inferioris prominens, dense hirsutotomentosa. Pedicelli usque ad 7 mm. longi, dense tomentosi. Tubus basalis calycis usque ad 9 mm. longus, lobi calycis obovati (15 × 9 mm.), extra pilis aureo-brunneis tomentosi, intus pilis aureo-luteis sericei. Petala cochleariformia (21 × 6 mm.), manifeste unguiculata. Ovarium stipitatum (3-6 mm. longum), pilis aureo-luteis, ad basem ovarium versus densioribus longissime obtectum. Fructus magni (9-15 cm. × 7-10 cm. × 2.5-3.0 cm.), complanati, pallide brunnei, ambitu porcis transversis summo rotundatis instructi, suturi haud perspicui. Semina 5 vel 8, vel plus.

HOLOTYPE. Una, Bahia, Brazil. Ca. 3 km. east of Fazenda São Raphael, Oct., 1969, Jean H. Langenheim 5644 (uc \*\*; isotype, uc). Feb., 1971, Yin-Tse Lee 164 (paratype, uc).

Tree to 28 m. tall, the trunk to ca. 90 cm. in diameter, evergreen to facultatively deciduous. Young branches, leaf buds, petioles and leaves covered with golden-yellow tomentum, golden-brown upon aging. Older branches brown to silvery gray, with peeling epidermis. Leaves shortpetiolate; petiole 3 to 7 mm. long. Stipules narrowly elliptic (15-20 mm. long, 5-8 mm. wide), obtuse, caducous. Leaflets oblique, sessile on one side and with petiolule ca. 3 mm. long on the other, coriaceous, obovateoblong, 5-9 cm. long, 2-4 cm. wide, obtuse to apiculate; sparsely puberu-

<sup>\*\*</sup> Upon completion of the systematic revision of the genus now in progress at the University of California, Santa Cruz, all specimens will be deposited in the herbarium of the University of California, Berkeley.

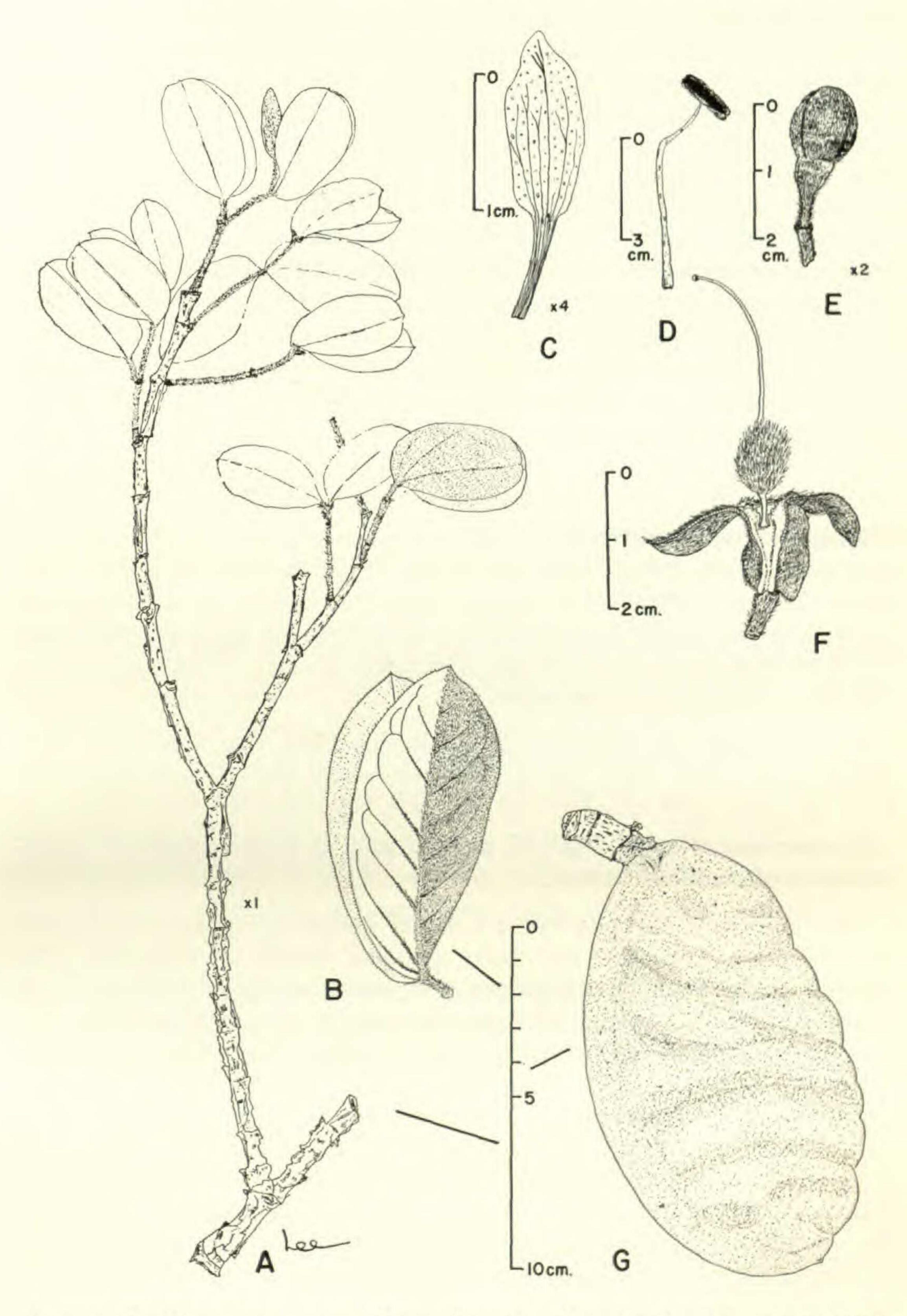


FIGURE 2. Hymenaea aurea. A, portion of a branch showing young leaves and tomentose branchlets; B, mature leaf; C, petal; D, stamen; E, mature flower bud; F, partly dissected flower showing position of stipe relative to hypanthium; G, slightly lateral view of fruit showing rounded ridges.

lent and shining above, densely pubescent beneath with golden-brown tomentum and prominent midrib which is densely hirsute-tomentose. Inflorescence a compound corymb; rachides short and robust, strongly flexuous. Bracts and bracteoles suborbicular, densely golden-brown tomentose dorsally, deep brown and glabrous within. Pedicels ca. 7 mm. long, densely tomentose. Flower medium in size for the genus. Calyx tube with stalk-like base (stalk ca. 9 mm. long); calyx lobes obovate (15 mm. long, 9 mm. wide), golden-brown tomentose dorsally, goldenyellow sericeous within. Petals creamy white, spatulate, 21 mm. long, 6 mm. wide, distinctly unguiculate (claws ca. 9 mm. long), caducous. Stamens ca. 30 mm. long; anthers elliptic, ca. 6 mm. long. Ovary with stipe 3 to 6 mm. long, oblique-oblong, heavily pubescent with golden-yellow woolly tomentum, the hairs longest at base; ovules 9 to 12; style ca. 25 mm. long, with minute capitate stigma. Fruit large and flat (9-15 cm. long, 7-10 cm. wide, 2.5-3.0 cm. thick), light brown, transversely ridged, suture not evident; seeds 5 to 8 or more.

Habitat and Distribution. This species is restricted to the Atlantic coastal evergreen forest. Although it was found in the same areas as H. oblongifolia var. latifolia (see below), along the eastern coast of southern Bahia, the two rarely occur together. It is frequent on clay-loam soils. The flowering season is from late December to early February. Fruits fall from November to December.

Brazil. Southern Bahia: Fazenda São Raphael, Una, Oct., 1969, J. H. Langenheim 5645, 5646, 5647. Along the eastern coast from Una to Eunapolia, Feb., 1971, Y. T. Lee 163, 177, 178, 180, 181, 182, 183, 184, 186.

Vernacular Names. "Jatobá peloso" and "jatobá verdadeiro" (eastern coast of southern Bahia).

This species is characterized by dense, golden-yellow tomentose hairs on the young branches, leaf buds, petioles, leaves, and flowers. The specific epithet is derived from the prominence of these golden hairs on many parts of the plant. This species can be distinguished from Hymenaea eriogyne Benth. by (1) the ovary which is densely tomentose, but never hirsute at the base and (2) its unusually flat fruits. In addition, despite its close relationship to the Amazonian hylaea species, H. eriogyne is a low tree and presently is restricted to the caatinga areas in north-eastern Brazil. Hymenaea aurea is distinguished from H. oblongifolia Huber, H. parvifolia Huber, and H. torrei Léon by its medium-sized flowers, corymbose inflorescence, and large fruits, and from the remainder of the species of Hymenaea by its densely tomentose ovary.

Hymenaea oblongifolia var. latifolia Lee & Langenheim, var. nov. Figures 1 and 3.

Var. oblongifolio similis, foliola multo latiora (longitudo/latitudo ca. 2:1), obtusa vel retusa, interdum breviter acuminata, alabastris floriferis oblongioribus (18 × 6 mm.), lobis calycis anguste ovatis, leviter acutis

(9-12 mm. longis), petalis manifeste unguiculatis, unguibus usque ad 8 mm. longis, sub anthesi erectis discedit.

Holotype. Itabuna, Bahia, Brazil. Along road between the main entrance and the library on the grounds of CEPEC, Jan. 1971, R. S. Pinheiro 1720 (CEPEC). Feb. 1972, Vin-Tse Lee 162 (isotype, uc). Both specimens were collected from the same tree which is still living on the grounds of CEPEC. Village of Rio Branco, near Una, Bahia, Oct. 1969, Jean H. Langenheim 5648 (paratype, uc).

Tree to 25 m. tall, the trunk to ca. 100 cm. in diameter, evergreen to facultatively deciduous. Leaves glabrous throughout; petioles rigid, 2-3 cm. long. Stipules narrowly-elliptic (15-20 mm. long, 5-8 mm. wide), obtuse, caducous. Leaflets oblique, sessile on one side and with petiolule ca. 6 mm. on the other, coriaceous, broadly oblong, 8-13 cm. long, 4.5-7.0 cm. wide (L/W ca. 2/1), obtuse to retuse or occasionally somewhat acuminate; midrib and secondary veins sharply prominent beneath. Inflorescence paniculate, the racemes ca. 18 cm. long; rachides golden-brown tomentose, ca. 5 cm. long at base of the inflorescence, slightly flexuous. Bracts and bracteoles suborbicular, 5 mm. long, caducous. Calyx tube broadly-obconic, with short stalk; calyx lobes narrowly ovate, 9 to 12 mm. long, slightly acute, about equally tomentose on the two sides. Petals creamy white, broadly spatulate (15 mm. long, 9 mm. wide), distinctly unguiculate (claws ca. 8 mm. long), erect during anthesis. Stamens ca. 25 mm. long; anthers elliptic, ca. 4 mm. long. Ovary with short stipe ca. 3 mm. long, compressed oblique-obovoid, densely hirsute, hairs longer at the base; style laterally attached, ca. 15 mm. long, glabrous, with minutely capitate stigma; ovules 3 to 4. Fruit ovoid to subcompressed obovoid (4.0-7.0 cm. long, 2.5-4.5 cm. wide, 2.5-3.5 cm. thick); suture not prominent; stalk ca. 12 mm. long; calyx occasionally remaining attached at base; seeds 1 to 3.

Habitat and Distribution. This variety is restricted to the Atlantic coastal evergreen forest which has been heavily cut for cultivation of cacao. It is most frequently found as isolated trees in cacao plantations (matta de cacau) or along rivers in the forest. It occurs particularly on sandy loam soils. The flowering season is from January to late February. Fruits fall around December.

Brazil. Pernambuco: Rio Gurjaú, vicinity of Recife, Dec. 1951, A. Ducke & D. Andrade-Lima 70 (IPEAN, R); Dec. 1952, D. Andrade-Lima 52-1197 (IPA). Southern Bahia. Village of Rio Branco, near Una, Oct. 1969, J. H. Langenheim 5649. Along the eastern coast from Una to Prado, Feb. 1971, Y. T. Lee 166, 167, 168, 169, 170, 171, 173, 175, 176, 179, 187.

VERNACULAR NAMES. "Jatobá burundanga" and "jatobá farinheira" (eastern coast of southern Bahia).

The new taxon first came to our attention during a trip made by one of us (JHL) in 1969. The close affinity with the Amazonian species H.

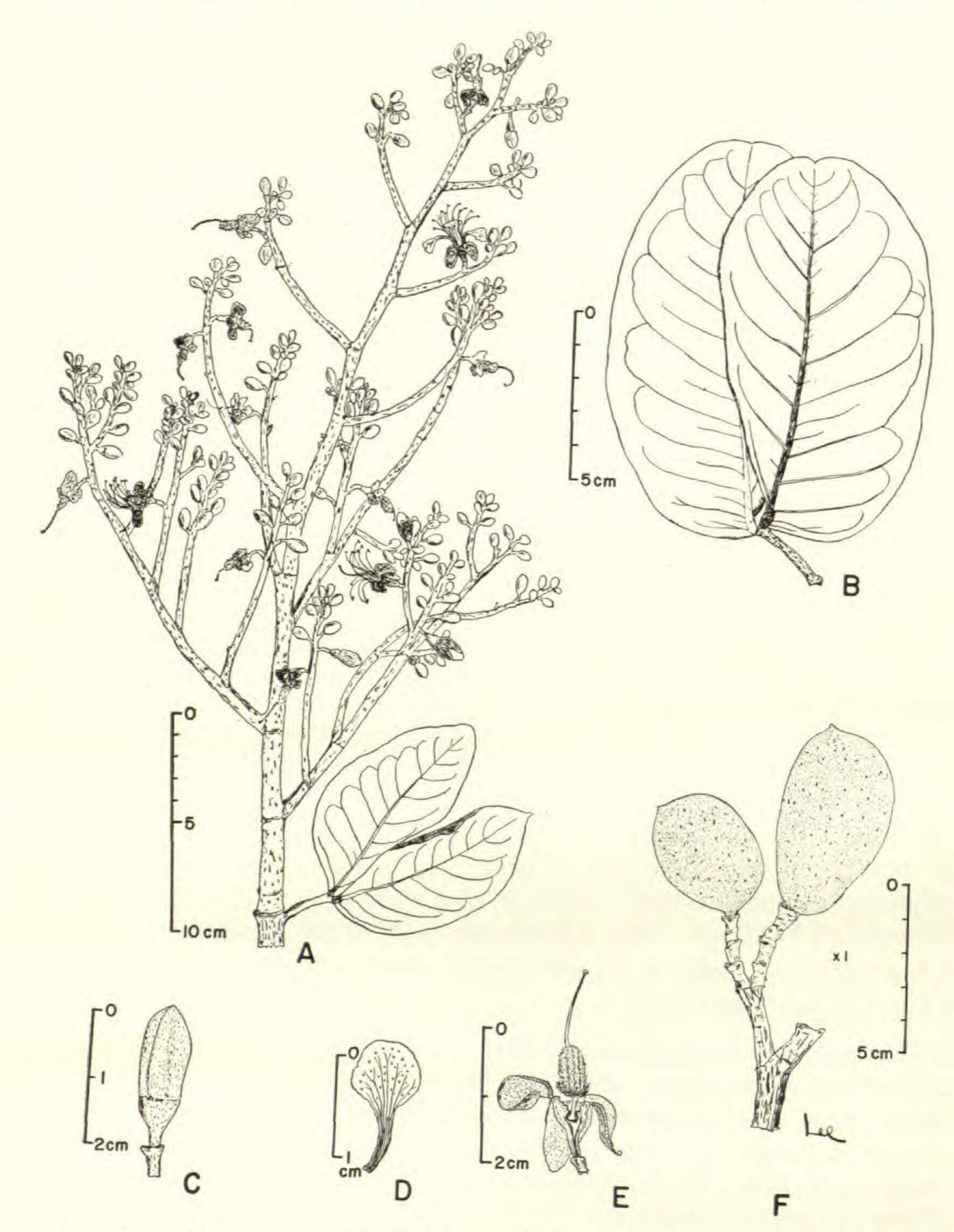


FIGURE 3. Hymenaea oblongifolia var. latifolia. A, inflorescence; B, mature leaf; C, mature flower bud; D, petal; E, partly dissected flower showing position of stipe relative to hypanthium; F, fruits.

oblongifolia Huber was immediately recognized, although the final determination was not made until flowers and the complete inflorescence were collected in 1971.

The epithet expresses the exceptional width of the leaflets. The name should not be confused with *H. latifolia* Hayne (Hayne, 1830), which has been appropriately transferred to the genus *Peltogyne* (Bentham, 1870).

In fact, the first two specimens of this variety were collected in the vicinity of Recife by the late Professor A. Ducke and Professor D. Andrade-Lima in the early fifties and were subsequently incorrectly identified by Ducke as *Hymenaea latifolia* Hayne.

The new variety is distinguished by the wide-oblong leaflets (the length-width ratio is about 2, as compared to 3 in var. oblongifolia), the distinctly unguiculate petals, and its habitat in the uplands of the Atlantic coastal evergreen forest.

Hymenaea oblongifolia var. palustris (Ducke) Lee & Langenheim, comb. et stat. nov. Figure 1.

H. palustris Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 24. 1915.

Holotype. In swamp forest (igapó) toward river margins. Utinga, near Belém, Pará, Brazil, Oct., 1914, Adolpho Ducke (мв) 15496 (мв, isotype, кв).

Tree to 30 m. tall, the trunk to ca. 85 cm. in diameter. Young branches sometimes rusty-tomentose. Petioles rigid, ca. 15 mm. long. Leaflets oblique, sessile on one side and with petiolule ca. 6 mm. long on the other, narrowly oblong (12–16 cm. long, 3.0–4.5 cm. wide), acute to obtuse, densely pubescent beneath with golden-brown tomentose hairs. Inflorescence paniculate, rachides rather long, slightly flexuous. Flowers smaller than in var. oblongifolia and var. latifolia. Pedicels ca. 2 mm. long. Calyx lobes ca. 7 mm. long, obtuse. About equally white-rusty sericeous on the two sides. Petals ca. 12 mm. long, subsessile. Stamens ca. 15 mm. long, anthers ca. 3 mm. long. Ovary short-stipitate, densely hirsute, hairs longer at base; ovules 3 to 4. Fruit ovoid to obovoid, subcompressed, suture not evident, short-stalked; seeds 1 to 3.

Habitat and Distribution. This variety is restricted to the swamp forest or igapó; it is from this habitat that it derives its name. It has essentially the same distribution as that of var. oblongifolia, occurring in the igapó, however, rather than the várzea. The flowering season is from September to October in Brazil and about a month later in Peru. Fruits fall around August.

Vernacular Names. "Jutaí" and "jutaí de igapó" (Pará and Terr. Amapá).

Brazil. Gurupú, Pará, Oct., 1916, A. Ducke (MG) 16567 (K, MG, R, US). Along Río Araguari, near Serro do Nevio, Terr. Amapá, Oct., 1961, J. M. Pires, W. Rodrigues, & G. C. Irwin 51392 and 51393 (IPEAN, MG); 51438 (COL, IPEAN, MG, R, UB, VEN); Nov., 1971, Y. T. Lee 67, 68, 69, 70 (UC). Ríos Pacaja and Muirapiranga, Pará, Oct., 1965, T. D. Pennington & N. T. Silva 1660 (IPEAN, K, NY, US).

Colombia. Río Yurumanguí, Dept. de Valle, Jan.-Feb., 1944, J. Cuatrecasas

15836 (COL, US).

Guyana. Upper New River, Dec., 1935, T. G. Myers 5868 (K); ?Schoenbaugh (K).

Peru. Río Itaya, Dept. Loreto, Sept., 1929, L. Williams 3453 (us). Quebrada Valentin-Río Tahuayo, Dept. Loreto, Sept.-Oct., 1963, A. A. Vargas 131 (NY, us).

As described by Ducke in 1915, *H. palustris* was distinguished from *H. oblongifolia* by small differences such as (1) hairs on the lower surface of the leaves, (2) narrower leaflets, (3) smaller flowers, and (4) much harder wood. These differences are sufficiently minor that Sandwith (1938) questioned whether or not *H. palustris* should be made a variety of *H. oblongifolia*. In the process of examining specimens for a systematic revision of the entire genus, we feel justified in reducing *H. palustris* to varietal status under *H. oblongifolia*.

Hymenaea oblongifolia var. davisii (Sandwith) Lee & Langenheim, comb. et stat. nov. Figure 1.

H. davisii Sandwith, Bull. Misc. Inf., Roy. Bot. Gard. Kew 1931: 366-367.

HOLOTYPE. In true Wallaba (*Eperua*) forest, along Warimia Creek, Essequibo River, Guyana, Jun., 1929, Forestry Department Record No. 943 (к).

Tree ca. 35 m. tall, the trunk ca. 60 cm. in diameter. Leaves glabrous throughout; petioles rigid, ca. 25 mm. long. Leaflets oblique, sessile on one side and with short petiolule ca. 5 mm. on the other, coriaceous, narrowly oblong, always distinctly falcate, 11 to 15 cm. long, 3.0 to 4.2 cm. wide, long acuminate. Inflorescence paniculate, to 15 cm. long; rachides pale brown tomentose, rather long and slightly flexuous. Pedicels 5–7 mm. long. Calyx tube obconical, with stalk-like base ca. 9 mm. long; calyx lobes elliptic-oblong, outside pale brown tomentose, inside dense, golden-brown sericeous. Petals oblong-lanceolate or lanceolate, 13–15 mm. long, 5–6 mm. wide, subsessile. Stamens 20–30 mm. long; anthers 4–5 mm. long. Ovary short-stipitate, densely hirsute, hairs longer at the base; style glabrous, 20–25 mm. long, with minute capitate stigma; ovules up to 6. Fruits ovoid (4.0–4.5 cm. long, 3.5 cm. wide), usually one-seeded.

HABITAT and DISTRIBUTION. This variety has been collected only twice along streams in the Wallaba forest, both times in the drainage of the Essequibo River, Guyana. Flowers in June.

VERNACULAR NAMES. Locust, simiri or courabarie, although the first two names also refer to the more common species, *H. courbaril*, in Guyana.

Guyana. Macouria River, Essequibo River, Mar., 1909, C. W. Anderson 165 (K).

Hymenaea davisii was named by Sandwith in honor of Mr. T. A. W. Davis, then Assistant Conservator of Forests, British Guiana. Sandwith recognized its close affinity to H. oblongifolia but characterized H. davisii by (1) narrowly falcate and long acuminate leaflets, (2) long pedicels, (3) long stalk-like base of the calyx-tube and (4) usually one-seeded

fruits. After examining the type specimen and evaluating all the characters, the differences listed are considered as trends within a rather diverse species complex. Thus, it is appropriate to reduce *H. davisii* to a varietal status under *H. oblongifolia*. *Hymenaea oblongifolia*, therefore, is considered to be a polymorphic species with four varieties. A synoptic key to the varieties is presented to aid in identification:

1. Leaflets glabrous on the two sides.

- 2. Leaflets narrowly or wide-oblong; petals subunguiculate to distinctly unguiculate; calyx-tube with short stalk-like base, ca. 3 mm. long.
  - 3. Leaflets elongate-oblong (L/W ca. 3); petals subunguiculate to unguiculate. ..... var. oblongifolia.
  - 3. Leaflets wide-oblong (L/W ca. 2); petals distinctly unguiculate. ... var. latifolia.
- 1. Leaflets with dense, golden-brown tomentose hairs underneath. .... var. palustris.

## ACKNOWLEDGMENTS

We wish to thank Dr. Paulo de T. Alvim, Director; Mr. Sérgio G. da Vinha, Mr. Maximo Hori, botanist and forester, of the Centro de Pesquisas do Cacau (CEPEC), Itabuna, Bahia, Brazil, for their generous support in providing assistance for the collection of the plants from Bahia. We are appreciative for the Latin descriptions done by Dr. Rimo Bacigalupi and criticism of the manuscript by Dr. Alva Whittingham. Also our gratitude is expressed to the curators of the herbaria, listed below with two exceptions by abbreviations of Lanjouw and Stafleu (1964), who kindly loaned or provided us facilities to examine specimens essential to this study; CEPEC, COL, IPA (Instituto de Pesquisas Agronômica, Recife, Pernambuco, Brazil), IPEAN, K, MG, NY, R, RB, UB, UC, US, and VEN. Grateful acknowledgment is made for funds to support this study from National Science Foundation grants GB-58161, GB-13659 and GB-29278.

## LITERATURE CITED

Andrade-Lima, D. Notas sôbre a dispersão de algunas especies vegetais no Brasil. An. Soc. Biol. Pernambuco 11(1): 25-49. 1953.

Bentham, G. Hooker's Journal of Botany 2: 74. 1840.

——. In: Martius, Fl. Brasiliensis 15(2): 232. 1870.

CANDOLLE, A. DE. Prodr. 2: 94. 1825.

Ducke, A. Estudos botânicos no Ceará. An. Acad. Brasil. Cien. 31(2): 211-308. 1959.

HARRINGTON, H. J. Paleogeographic development of South America. Am. Assoc. Pet. Geol. Bull. 46: 1773-1814. 1962.

HAYNE, F. G. Arzneikunde gebraüchlichen gewächse 11: 7. Berlin. 1830. Heywood, V. H. The Leguminosae—a systematic purview. In: Chemotax-

onomy of the Leguminosae. Eds. J. B. Harborne, D. Boulter & B. L. Turner. Academic Press, New York. 1-29, 1971.

Lanjouw, J., & F. A. Stafleu. Index herbariorum, 5th ed. Int. Bur. Pl. Tax. and Nomencl., Utrecht, Netherlands. Regnum vegetabile: 31. 1964.

- LANGENHEIM, J. H. Leguminous resin-producing trees in Africa and South America. In: Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Eds. B. J. Meggars, E. S. Ayensu & W. D. Duckworth. Smithsonian Press, Washington, D.C. 1972.

Léonard, J. Genera des Cynometreae et des Amherstieae Africaines. Mem. Classe des Sciences de l'Academie Royale de Belgique 30(2): 1-314. 1957.

Menéndez, C. A. Die Fossilen Floras Südamerikas. In: Biogeography and Ecology in South America, vol. 2. Eds. E. F. Fittkau et al. Dr. W. Junk Publ. The Hague. 519–561, 1969.

RIZZINI, C. T. Notas prévia sôbre divisão fitogeográfica do Brasil. Revista Bras. Geol. 25(1): 3-64. 1963.

———. Delimitação e relações da flora silvestre hileiana. In: Atas do Simpósio sôbre a Biota Amazônica, vol. 4 (Botânica). Ed. H. Lent. Conselho Nacional de Pesquisas, Rio de Janeiro. 13-36. 1967.

Sandwith, N. Y. New species and records from British Guiana. XV-Contributions to the flora of tropical America: XXX. Bull. Misc. Inf. Roy. Bot. Gard. Kew 1937(2): 100-112. 1938.

SIMPSON, G. G. South American mammals. In: Biogeography and Ecology in South America, vol. 2. Eds. E. F. FITTKAU et al. Dr. W. Junk Publ. The Hague. 879–909. 1969.

Vanzolini, P. E., & E. E. Williams. South American anoles. The geographic differentiation and evolution of the *Anolis crysolepis* species group (Sauria Iguanidae). Arq. Zool. São Paulo 19(142): 1-124. 1970.

Wolfe, J. A. Tertiary climate fluctuations and methods of analysis of Tertiary floras. Paleogeography, Paleoclimatol., Paleoecol. 9: 27-57. 1971.

DIVISION OF NATURAL SCIENCES
UNIVERSITY OF CALIFORNIA
SANTA CRUZ
CALIFORNIA 95060